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BLOAT IN CATTLE

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BLOAT IN CATTLE¹

H. H. COLE,² S. W. MEAD,³ AND MAX KLEIBER⁴

BLOAT, the overdistention of the first two stomachs with gas, is a serious problem in cattle and sheep production. It offers a real obstacle in the pasturing of legumes such as the clovers and alfalfa. Because, from a nutritive standpoint, legume pastures are particularly valuable, determining how they may be safely used is important. Bloat may occur on

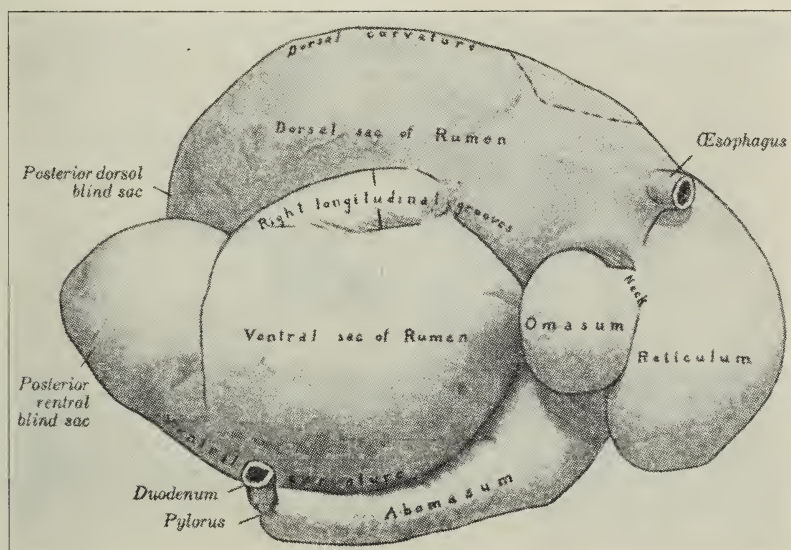


Fig. 1.—The four stomachs of the ruminant (sheep) viewed from the right side. (Reproduced from: Sisson and Grossman, *Anatomy of the Domestic Animals*, with the permission of W. B. Saunders Co., Philadelphia, Pa., the copyright owners.)

several other succulent feeds, including tubers and roots. Occasionally an individual sheep or cow will bloat on any type of ration. Such animals are chronic bloaters, perhaps for causes other than those considered in this discussion.

In order to develop sound precautionary measures, one must understand the causes of bloat. Our studies, though they do not give a complete answer, clarify the problem considerably.

For an understanding of the subject, certain facts regarding the anat-

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omy and physiology of the ruminant stomachs are important. The four stomachs are the rumen, reticulum, abomasum, and omasum (fig. 1). In bloat, we are primarily concerned with the first two—the rumen and the reticulum—although their free communication (fig. 2) makes them practically a unit. The four stomachs of the cow hold 20 to 40 gallons, the exact amount depending upon the size of the animal. The rumen is by far the largest, accounting for about 80 per cent of the total capacity, according to Schalk and Amadon (11).⁵

No digestive enzymes are swallowed by the cow in its copious saliva (12) or secreted directly by the rumen (3). Perhaps this statement is too

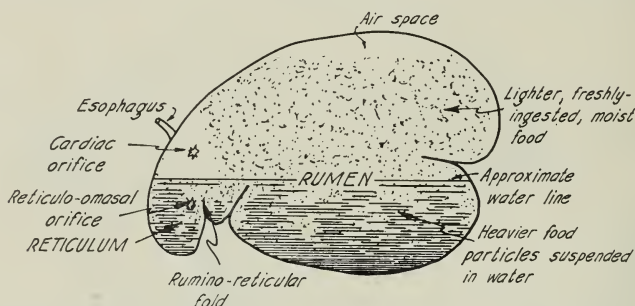


Fig. 2.—Diagrammatic sketch of the midlongitudinal section of the rumen and reticulum adapted from Schalk and Amadon (11). The opening of the esophagus into the rumen (cardiac orifice) is on the right side of the rumen, as is the opening of the reticulum into the omasum (reticulo-omasal orifice). Note that the rumen and reticulum are only partially separated by the rumino-reticular fold; also that the reticulo-omasal orifice is submerged in liquid, whereas the cardiac orifice is not. A syringelike action of the reticulum tends to force freshly swallowed food into the posterior rumen.

dogmatic, for Wise, Miller, and Anderson (16) have shown that milk undergoes some changes while passing through the mouth and esophagus of the calf.

Food within the rumen and reticulum is softened and reduced to a pulp by the rhythmic muscular contractions of the rumen and is ground and further macerated by the rumination process. It takes about 60 hours to empty the rumen. Bacteria, yeasts, and other microorganisms carry on extensive fermentative and digestive action that results in the liberation of abundant carbon dioxide and methane, or marsh gas, with smaller amounts of hydrogen, hydrogen sulfide, and carbon monoxide. We shall later show how the rate of formation of carbon dioxide and methane is related to the kind and amount of food ingested, and shall also consider some facts regarding the control of the belching mechanism.

Because of the many similarities between belching and the regurgitation of food for rechewing, we should like to consider the whole rumi-

⁵ *Italic numbers in parentheses refer to "Literature Cited" at the end of this bulletin.*

nation process briefly, for the details of its mechanism have been rather completely worked out. On a ration of hay and grain, a cow will ruminate about 6 hours daily. As she spends approximately the same amount of time in eating, she is either eating or ruminating 12 hours out of every 24 (11). The amount of rumination depends on the nature of the feed. Mead and Goss (7) found, for example, that cows on grain alone ruminated very little.

Shalk and Amadon (11) have furnished the most exact knowledge regarding the regurgitation mechanism and its control. They showed that regurgitation proceeds as follows: first, an extra strong contraction of the reticulum floods the esophageal opening into the rumen with a soupy material; at the same time, a strong inspiratory movement, drawing air into the lungs, reduces the pressure within the thorax and therefore within the esophagus (since the esophagus passes through the thorax in reaching the rumen). This reduced pressure sucks the soupy material into the esophagus, and finally a reverse-peristaltic wave along the esophagus carries the material to the mouth. The cow then squeezes the water out of this regurgitated mass, swallows the water, and continues mastication. Obviously, therefore, regurgitation involves the coördinated activity of the muscles of the reticulum, diaphragm, and esophagus. The muscles of the reticulum are entirely involuntary; those of the esophagus partly so. Regurgitation represents, then, a finely adjusted reflex act.

The next question involves the means of bringing on this reflex. As Schalk and Amadon showed, the act can be initiated by scratching the rumen wall with a wisp of hay through an artificial opening made into the rumen of the cow. The feeding of grain alone is not accompanied by a normal period of rumination. This fact is explained by the absence of an adequate amount of fibrous material contacting the wall of the rumen and initiating the reflex. The inference is clear, therefore, that the scratching action of ingested roughage on the anterior wall of the rumen normally initiates rumination.

No attempt is made here to review the literature on the physiology of the ruminant stomach. Certain papers, however, will prove helpful as a source of references: Quin, van der Wath, and Myburgh (10), Quin and van der Wath (9), and Dukes (3) cite much of the literature on ruminal motility. Washburn and Brody (15) have reviewed that dealing with gas formation in the rumen. Mangold (6) gives a comprehensive bibliography on the digestion of cellulose. Olson (8) refers to many of the papers on bloat.

We shall first present the results of our investigations and then discuss, in the light of these studies, the theories on the cause of bloat, together with measures useful in preventing bloat.

EXPERIMENTAL METHODS AND RESULTS

Most of the gas formed within the rumen is expelled by belching. A smaller amount diffuses into the blood stream and is expelled through the lungs. To gain information on the frequency of belching, we recorded the number of audible eructations in a cow over 9-hour periods while receiving daily (a) all the hay she wanted and 5 pounds of grain, (b) 21 pounds of green alfalfa alone, and (c) 12 pounds of concentrates alone. The cow was kept on the different rations for at least a week before the observations were made. On the hay and grain ration, the average number of eructations was 10.7 per hour, for the green alfalfa alone 9.3 per

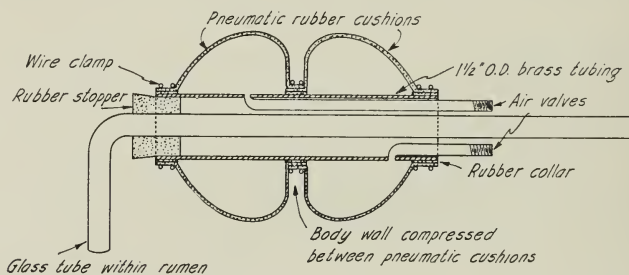


Fig. 3.—Diagram of the plug used to close the rumen fistula. When used for gas studies, the glass tube extending through the plug was used to connect the interior of the rumen with a mercury manometer or gas meter. When being used simply to seal off the rumen, the glass tube with its stopper was removed, and a solid cork stopper substituted. The diameter of the glass tube is 8 mm. To seal off effectively the cavities to which the air valves lead, a piece of thick rubber tubing was first pulled over the brass tubing at the center and at the two ends. Then the pneumatic cushions were cemented to this rubber tubing, and wire clamps used to make it more secure. These wire clamps were covered with bicycle tape and then with soft, thin rubber tubing. The brass tube is 6½ inches long.

hour, and for the concentrates alone 5.3 per hour. With all the rations used, there was a definite increase of belching soon after feeding began, and this increased rate was maintained for 2 to 4 hours. As will be shown, the rate of gas formation is increased during this same period, and thus the increased rate of belching is explained. This preliminary observation that belching occurs as frequently on hay and grain as on green alfalfa led to the study of the rate of gas formation.

The Relation of Ruminal Activity to Belching.—In human beings, belching is in part a voluntary act largely dependent upon a simultaneous contraction of the diaphragm and abdominal muscles, which increases the pressure on the stomach and causes the gas to be forced out. In the cow the diaphragm and abdominal muscles do not assist in the act. This fact led to a study of the action of the ruminal musculature itself. Schalk and Amadon (11) recorded ruminal motility in the ox by

inserting one or more toy balloons through a rumen fistula and holding the partially inflated balloon against the part of the rumen wall to be studied. By holding two balloons simultaneously against different portions of the rumen, they determined the sequence of muscular activity within the rumen. The balloon was attached to a water manometer, and the variations in pressure were recorded on a kymograph drum. This method is satisfactory for determining the sequence of activities within the rumen. Schalk has also recorded the ruminal motility with a movie camera.

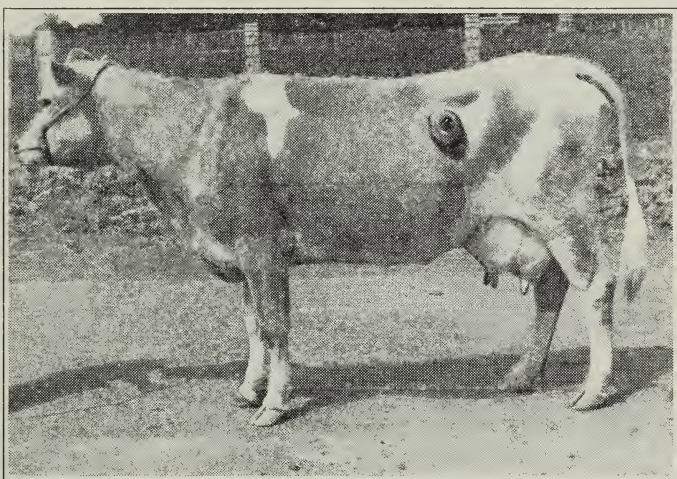


Fig. 4.—The plug diagrammed in figure 3 closing the ruminal fistula of cow 557. This cow has delivered two normal calves and gone through two lactations since the ruminal fistula was established.

Since, however, these methods require that the rumen be left open, they prevent determination of the relation between ruminal contractions and belching. We therefore devised a method of recording ruminal pressures and, with the knowledge gained by previous workers, were able to relate these pressures to the activity of a given portion of the rumen. This method also allowed us to determine the exact time at which the pressure dropped because of belching.

In these studies we used a cow with a permanent ruminal fistula. An airtight plug (fig. 3) has been devised for the fistula with a tube extending through it to connect the rumen with a mercury manometer. The shaped pneumatic cushions are made by use of a steel mold. This plug is used to close the fistula at all times (figs. 4 and 5). When experiments are not in progress, it is deflated somewhat so that the opening is not airtight. If sufficient pressure for perfect tightness is maintained for an

extended period, some necrosis results around the fistulous opening. The pressures were determined simply by connecting the glass tube of the ruminal plug to a mercury manometer with pressure tubing. The changes in pressure were recorded on a kymograph drum.

Figure 6 shows a pressure curve, with the occurrences of belching noted on it. The drop in pressure due to belching follows a ruminal contraction, although belching does not occur at each ruminal contraction. The exact phase of ruminal motility at which the pressure becomes greatest and belching occurs is most easily determined in the cow during rumination,

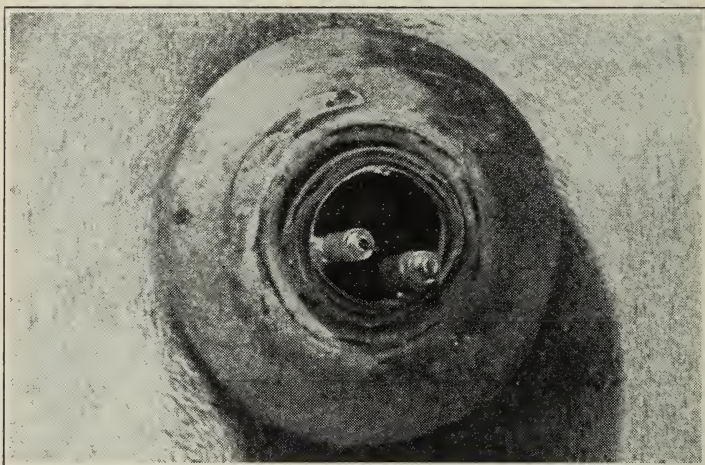


Fig. 5.—A nearer view than figure 4, of the plug closing the ruminal fistula. As shown here, the glass tube extending through the core of the plug is removed if the plug is being used simply as a means of sealing off the fistulous opening.

for Schalk and Amadon showed that the reticulum is contracted and the rumen relaxed at the moment of regurgitation. There is no appreciable change of ruminal pressure as food is regurgitated; the rise comes 6 to 10 seconds later as the rumen undergoes contraction. Quin and van der Wath (9), studying ruminal pressures in a similar manner, but with a somewhat different type of plug, devised by Quin, van der Wath, and Myburgh (10), have noted that, in sheep, belching is related to ruminal contraction.

The fact that belching is related to ruminal contraction is important for an understanding of the mechanism. Since, however, belching does not occur at each ruminal contraction, other factors are evidently involved.

Ruminal Pressure and Belching.—The fact that belching occurs when the ruminal pressure is greatest, that is, at the peak of ruminal contrac-

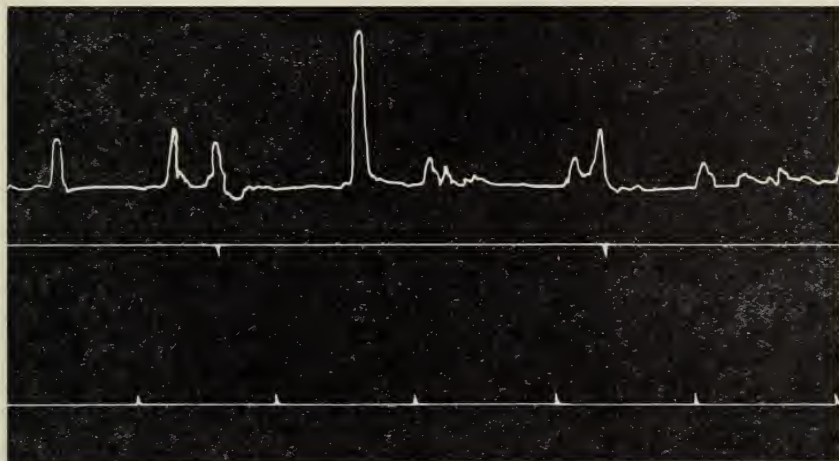


Fig. 6.—Tracing of portion of ruminal pressure curve of cow 557 on full ration of alfalfa hay and corn silage, using mercury manometer (January 29, 1937). The bottom line is the time interval in minutes. The points on the middle line indicate when audible belching occurred. The vertical scale represents pressure, 0.5 mm on the graph corresponding with 1.0 mm mercury of pressure. Note that after each belching a drop in ruminal pressure occurred and that this drop in pressure follows a ruminal contraction. The highest pressure point is due to stretching. Stretching, coughing, and so forth, cause greater changes in ruminal pressure than does the contraction of the rumen musculature itself.

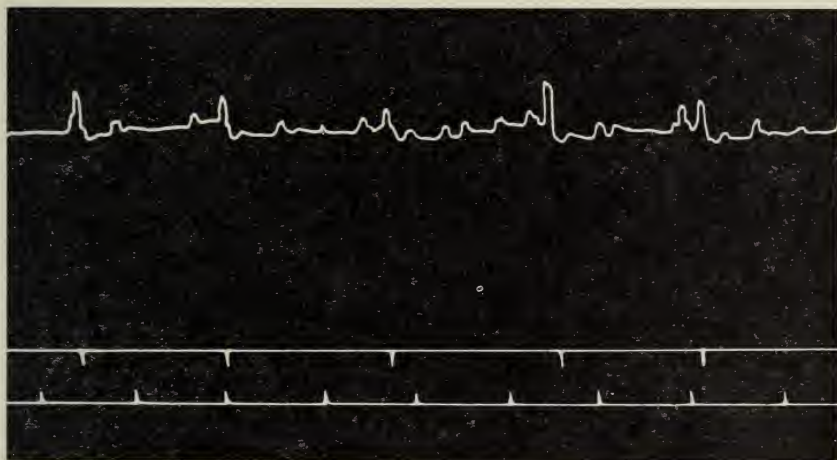


Fig. 7.—Tracing of portion of ruminal pressure curve of cow 557 while oxygen is being added at the rate of 3.6 liters per minute, using mercury manometer (April 13, 1937). As in figure 6, the bottom line is the time interval in minutes, the points on the middle line indicate when audible belching occurred, and the vertical scale represents pressure, 0.5 mm on the graph corresponding with 1.0 mm mercury of pressure. Though the ruminal pressure, during ruminal relaxation, is 8 mm mercury above the pressure before oxygen was introduced, belching still occurs only at the peak of ruminal contraction.

tion, indicates the importance of pressure. On this point, further evidence was secured by preventing a pressure increase during ruminal contraction. This was accomplished by aspirating gas from the rumen, through maintaining a slight negative pressure, in which case belching did not occur. The apparatus employed was the same as that used in studying the rate of gas formation (fig. 8). The aspirator is not necessary provided the outlet from the rumen is large enough to allow the gas to escape readily and thus equalize the pressure as the rumen decreases in size by contraction.

Pressure alone is not responsible for belching, however, as we have demonstrated by artificially increasing the pressure through forcing gas into the rumen. As figure 7 shows, under conditions of artificially increased pressure, belching occurred only during ruminal contraction, even though the pressure was greater during ruminal inactivity than the pressure associated with belching under normal conditions. This fact proves that the cardiac orifice guarding the entrance of the esophagus to the rumen is not automatically forced open whenever the pressure is increased to a certain point. Obviously, therefore, the other important factor in belching in ruminants is the reflex opening of the cardiac orifice. The role of the cardiac orifice in belching will be discussed later (p. 18).

Studies on the Rate of Gas Formation in the Rumen.—The rate of gas formation with various rations was studied in order to determine whether the frequency of bloat on legume pastures is simply the result of an excessive gas formation. Both a cow with a permanent ruminal fistula (cow 557) and a normal cow (cow 622), studied by means of a trocar canula, were used.

The rate was determined first in the animal with the ruminal fistula. An objection to the results with this animal could be made because, before each test period, the rumen was not sealed from the outside air, and consequently the ruminal flora might not be normal. Conceivably, this condition might have affected both the absolute and the comparative amounts of gas formed. Another objection to the results with this animal came to light during the investigation. When, during each test period, the gas from the rumen was sampled and analyzed, the carbon dioxide was sometimes distinctly lower and the oxygen higher than most of the analyses found in the literature. As was shown later, however, the total amount of gas formed with the ruminal-fistula animal was very similar to that obtained with the normal animal.

Figure 8 shows the apparatus used in determining the rate of gas formation. To avoid letting fluid pass into the gas meter, a trap was inserted to catch the fluid forced out of the rumen with the gas. A check valve was used to prevent the backward flow of gas during ruminal relaxation,

though its use in conjunction with the aspirating bottles is not absolutely essential. In the early studies, when no aspirator was used, air was sucked back through the gas meter from the outside air into the rumen during ruminal relaxation. This fact demonstrated that the pressure in the rumen during relaxation is below atmospheric (actual measurements show it to be -6 to -12 cm of water). According to Quin, van der Wath, and Myburgh (10), there is a "negative pressure" in the relaxed rumen of sheep. The gas meter used is the one commonly employed in metabolic tests. The aspirating bottles (so-called "Mariotte" bottles) were used to draw the gas out more rapidly during ruminal contraction

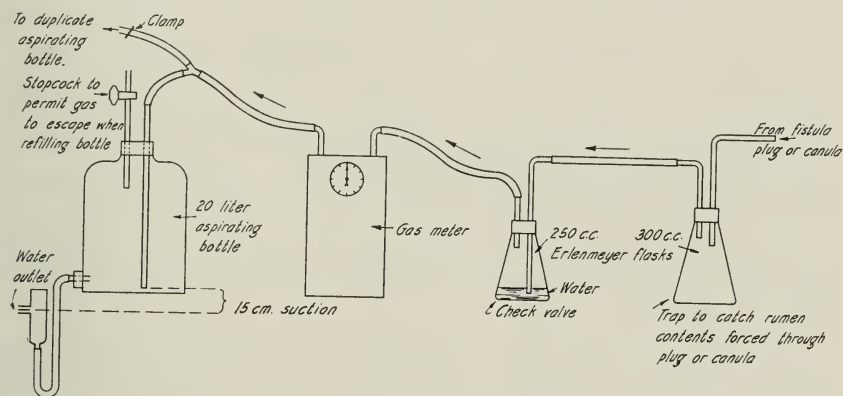


Fig. 8.—Schematic drawing of apparatus used in studying the rate of gas formation.

and thus avoid belching. Presumably, the suction created by the aspirating bottle might be sufficient to draw air through the esophagus into the rumen. The analysis of gas samples taken during each test period showed, however, that this did not occur, since gas samples drawn from the rumen by this procedure were comparable to those taken directly from the rumen without previous aspiration.

In actual tests, the aspirating bottle proved unnecessary to prevent belching in the ruminal-fistula cow, whereas it was necessary with the canula in the normal cow because of the smaller size of the canula. The glass tube leading to the rumen through the fistula plug had a diameter of 8.0 mm, as compared with 4.5 mm for the bore of the canula used in the normal animal. Because of the larger opening, gas left the rumen freely during ruminal contraction, so that pressure was not sufficient for belching. The use of the aspirating bottle with a suction of 15 cm of water was enough to prevent belching in the normal animal except on one or two occasions when the canula became partly plugged with rumen contents.

We have compared the rate of gas formation on cut green alfalfa, alfalfa hay alone, and alfalfa hay and concentrates. The green alfalfa was cut rather than pastured in order that we might accurately determine the amount consumed. Lactating cows with greater appetites were used so that maximum food consumption occurred, since it is under this condition that bloat is most frequently encountered. The cow was kept on the particular ration to be studied, with excess feed provided, for at least 5 days before observations were made. The amount consumed on the day preceding the test always exceeded the amount on the day of the test, because feed was withheld during most of the test period. On March 18, for example, cow 622 ate 113 pounds of green alfalfa, whereas she ate only 24 pounds in the allotted 2-hour feeding period on the following morning during a test run (trial 2, green alfalfa, table 1). On March 24 she ate 12½ pounds of alfalfa hay and 21 pounds of concentrates, whereas on the morning of March 25, during a test run, she ate 9½ pounds of concentrates and no hay (trial 1, hay and concentrates, table 1). On March 27 she ate 5½ pounds of hay and 25 pounds of concentrates, whereas on the morning of March 28, during a test run, she ate 6 pounds of concentrates and 2 pounds of hay (trial 2, hay and concentrates, table 1).

The trocar was inserted in the normal cow every few days with no apparent ill effects. With one cow, in fact, seven insertions were made in one month, after which she continued to consume daily 10 pounds of alfalfa hay and 25 pounds of concentrates. Obviously, therefore, the treatment did not impair her appetite or well-being.

Table 1 shows the rate of gas formation in the normal cow. Results under comparable conditions with the ruminal-fistula cow were as follows: the average of four trials on green alfalfa was 71.21 liters for the period extending from 11 a.m. to 4 p.m. as compared with 64.04 liters for the normal cow; the average of three trials on alfalfa hay for the same period was 74.27 liters, as compared with 77.04 for the normal cow. In neither animal did gas formation on green alfalfa appear greater than for alfalfa hay or, in the case of the normal cow, for alfalfa hay and concentrates. In both animals a gradual decline in rate of gas formation began the fifth hour after feeding. The one exception was an increase in cow 622 between 3 p.m. and 4 p.m. on hay and concentrates. The reason for this increase is not entirely apparent. In one instance the cause may have been the plugging of the canula during the previous hour.

On the basis of these data, bloating on green alfalfa cannot well be attributed simply to excessive gas formation. In fact, the tendency seems to be for less gas to be formed from green alfalfa than from alfalfa hay and concentrates.

The rapid rise in gas formation after eating shows why bloating may occur soon after animals are turned onto alfalfa pasture. This rise is more clearly illustrated in figure 9 than in the table, for the amount of gas formed during the period of eating is shown.

TABLE 1

RATE OF GAS FORMATION IN COW 622 WHEN FED GREEN ALFALFA ALONE, ALFALFA HAY ALONE, AND ALFALFA HAY AND CONCENTRATES

(On the morning of the test, the cow was given all she would eat between 8 a.m. and 10:30 a.m.; in the evening all she would eat between 4 p.m. and 5 p.m.)

Ration fed	Feed consumed 8 a.m. to 10:30 a.m.		Feed consumed 4 p.m. to 5 p.m.		Gas produced							
	Rough-age	Concentrates	Rough-age	Concentrates*	11 a.m. to 12 m.	12 m. to 1 p.m.	1 p.m. to 2 p.m.	2 p.m. to 3 p.m.	3 p.m. to 4 p.m.	4 p.m. to 5 p.m.	5 p.m. to 6 p.m.	Total 11 a.m. to 4 p.m.
	pounds	pounds	pounds	pounds	liters	liters	liters	liters	liters	liters	liters	liters
Green alfalfa:												
Trial 1...	36	0	16	0	14.58	11.75	8.61	9.43	10.18	24.43	38.54	54.55
Trial 2...	24	0	14	0	18.51	16.24	17.00	12.69	9.09	—	—	73.53
Average...	30	0	15	0	16.55	14.00	12.81	11.06	9.64	—	—	64.04
Alfalfa hay:												
Trial 1...	6	0	4	0	26.18	20.32	15.77	11.74	12.74	23.96	—	86.75
Trial 2...	5	0	—†	—†	15.20	16.19	14.02	10.37	11.55	—	—	67.33
Average...	5½	0	—	—	20.69	18.26	14.89	11.06	12.15	—	—	77.04
Alfalfa hay and concentrates:												
Trial 1...	0	9½	0	5	14.87	30.30	15.72	1.23‡	22.01	25.57	30.98	84.13
Trial 2...	2	6	0	5	24.81	19.13	14.54	15.39	29.35	37.03	—	103.22
Average...	1	7¾	0	5	19.84	24.72	15.13	—	25.68	31.30	—	93.68

* The concentrate mixture consisted of 500 pounds rolled barley, 150 pounds dried molasses beet pulp, 100 pounds choice cottonseed meal, 8 pounds bone meal, and 8 pounds salt (NaCl).

† The canula was accidentally pulled out of the rumen, which terminated this trial prematurely.

‡ The canula became plugged during this period.

The following incident illustrates the rapidity with which bloating may occur after eating. On September 13 the ruminal-fistula cow was connected to the gas meter for gas-formation studies at 6 a.m. On the day previous she had received 71 pounds of green alfalfa. At 8 a.m. she was given 37 pounds of green alfalfa, and at 8:50 a.m. had consumed 15 pounds. Between 8:30 and 8:50 a.m. the glass tube leading to the rumen became partially plugged, and at 8:50 she was distinctly bloated and uncomfortable. Even though 16.8 liters of gas had escaped from the rumen during this period, the lack of sufficient stimulus to induce belching (see p. 18) had resulted in the retention of sufficient gas in the rumen

to produce marked bloating. Clearing of the glass tubing with a syringe bulb brought immediate relief.

To determine the relation between the amount of feed consumed and the amount of gas formed in the rumen, the feed intake in one experimental animal was lowered to 4 pounds of alfalfa hay daily. On the fourth day of this level of feeding, gas formation was determined as in the trials already described. In the period extending from 11 a.m. to 4 p.m., 11.08 liters of gas was formed as compared with an average of 77.04 liters for two previous trials on a full ration of alfalfa hay. Thus

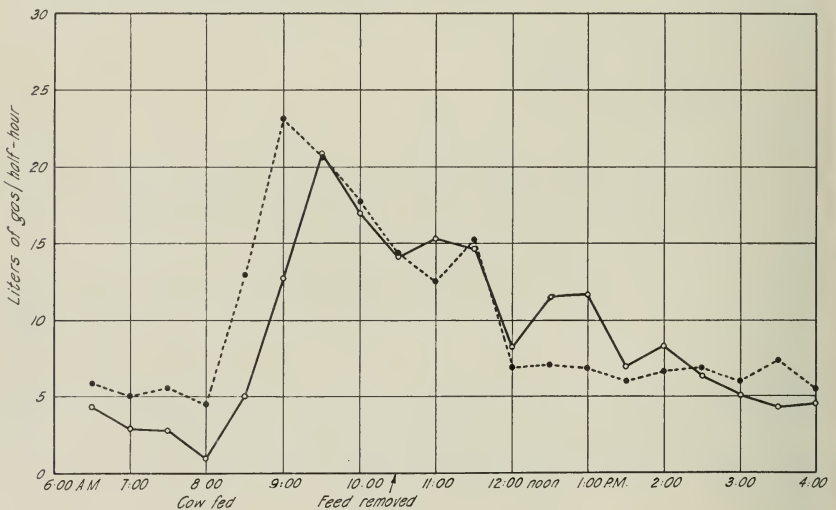


Fig. 9.—The rate of gas formation on green alfalfa alone and upon alfalfa hay alone in cow 557, expressed in liters per half-hour period. The solid line represents the average of five trials on a full feed of green alfalfa; the broken line, the average of three trials on a full feed of alfalfa hay.

a reduction in hay consumed from 25 pounds to 4 pounds daily resulted in a reduction in the amount of gas formed to one seventh. Apparently, therefore, feed consumed has a direct relation to gas formed. It is generally agreed among stockmen that greedy feeders are more likely to bloat than poor feeders; and one would expect lactating cows or rapidly growing animals to be particularly subject to bloat for the same reason.

Nature of Gases Formed in the Rumen.—During the gas-formation studies on the normal cow, we have determined the amount of carbon dioxide, methane, and oxygen present in the gas samples from the rumen. From the gas that flows out of the rumen, a sample is taken by letting mercury flow out of a glass bulb connected to the tube between rumen and testmeter. This gas sample is analyzed in an apparatus which we built especially for this purpose. Carbon dioxide and oxygen content of

the sample are first measured by absorption in sodium hydroxide and pyrogallol, respectively, and by determination of the changes in volume at a given constant pressure. The remainder of the sample is then mixed with pure oxygen, and this mixture is slowly pumped through a silica capillary tube which contains a glowing nichrome wire. The combustible gases—especially methane—are oxidized at the surface of this wire. The water and carbon dioxide formed are absorbed by driving the gas sample

TABLE 2
COMPOSITION OF RUMEN GAS IN COW 622 ON DIFFERENT RATIONS

Ration and time after feeding	Sample no.	Carbon dioxide	Oxygen	Methane	Other gases
		<i>per cent</i>	<i>per cent</i>	<i>per cent</i>	<i>per cent</i>
Alfalfa hay:					
2.5 hours.....	30	65.0	1.8	28.5	4.7
3.5 hours.....	18	63.3	2.0	22.0	12.7
4.0 hours.....	20	54.6	4.4	17.5	23.5
5.5 hours.....	32	73.2	1.4	25.1	0.3
6.0 hours.....	31	66.5	1.0	24.6	7.9
6.0 hours.....	29	67.6	1.1	23.7	7.6
7.5 hours.....	19	45.9	5.8	15.7	32.6
Average.....	..	62.3	2.5	22.4	12.8
Green alfalfa:					
2.5 hours.....	23	67.5	2.1	24.0	6.4
5.5 hours.....	22	68.5	1.1	21.0	9.4
Average.....	..	68.0	1.6	22.5	7.9
Alfalfa hay and grain:					
2.5 hours.....	24	68.2	2.3	9.2	20.3
2.5 hours.....	26	69.4	1.1	21.3	8.2
5.0 hours.....	25	73.3	1.0	18.9	6.8
6.0 hours.....	27	72.3	1.1	18.9	7.7
Average.....	..	70.8	1.4	17.1	10.8

through concentrated sulfuric acid and then through sodium hydroxide solutions. The increase of weight of the sodium hydroxide solution is used as a measure of the carbon dioxide produced by the combustion.

Table 2 presents the results. The amounts of these gases do not vary markedly with the different feeds used.

Washburn and Brody (15), who have the most complete data on the composition of rumen gases, have shown distinctly that the composition of rumen gases varies more with the time interval after feeding than with the ration. They obtained very similar results with three rations: alfalfa hay alone, alfalfa hay and grain, and grass. In each case, carbon dioxide was reduced from about 65 per cent at 4 hours after feeding, to 10 to 28 per cent at 15 to 23 hours after feeding. The percentages of oxygen and nitrogen rose as that of carbon dioxide decreased. The per-

centage of methane remained fairly constant. These results were obtained by feeding at approximately the maintenance level.

Dougherty (2) has suggested that an increase in the amount of carbon monoxide may be a contributing factor in causing death by bloat. As he definitely shows, if carbon monoxide is artificially introduced into the rumen, it will pass into the blood and decrease the oxygen-carrying capacity of the blood. But neither his results nor Olson's (8) indicate that the percentage of carbon monoxide varies with the type of food eaten.

Olson gives some data on rumen-gas composition of bloated animals. The average of nine samples taken from cows bloated on sweet clover was 61.97 per cent carbon dioxide, 3.61 per cent oxygen, and 18.42 per cent methane. Evidently, therefore, gases from his bloated animals do not differ strikingly from those obtained with our normal animals. As he explains, his oxygen figures are rather high because of the method of collecting samples.

Studies on the Artificial Introduction of Gas into the Rumen.—We have determined how much gas is produced in the rumen under maximum feeding conditions. The question arises: Do these amounts represent the maximum amount of gas that the cow can expel through belching under normal conditions without suffering serious bloat?

Carbon dioxide, methane, and oxygen were introduced separately into the rumen when the animal was on green alfalfa and also when it was on hay and grain. Unfortunately the same cow was not used on the two types of feed. We found that any of these gases could be introduced at the rate of 5 liters per minute and sometimes at the rate of 7 liters per minute for 30 minutes without prostration. In some instances it became necessary, at the higher rate, to discontinue introducing the gas after 10 minutes. At times the ruminal pressure rose to 100 mm mercury, but this increase was followed by belching and temporary relief. The introduction of carbon dioxide markedly affected respiration; after ruminal contraction the breathing became periodic and forced. This relation of forced breathing to ruminal contraction has not been explained; it is doubtless involved with belching, which involves both ruminal contraction and an inspiratory movement.

The most significant finding in these gas-introduction studies is that 150 liters of gas can be introduced within a half hour without serious results, whereas it would take several hours for this amount of gas to be formed naturally.

DISCUSSION

The experiments will be discussed in the light of some of the more commonly accepted theories of bloat.

Excessive Gas Formation.—One commonly accepted theory of bloat is that an excessive amount of gas is formed in the rumen and that this is most likely to occur when cows are pastured on green legumes. Veech (13) assumes, for example, that bloat is due to succulent foods in the rumen, which cause the formation of large quantities of gas. Gallagher (4) states that the rapid formation of a large quantity of gas in the paunch causes bloating. Viljoens (14) suggests that bloat commonly results from an excessive production of gases or from an abnormal accumulation due to the absence of active movements of the walls of the rumen. According to Woodward and Dawson (17), any feed that produces indigestion and forms gas in the stomach may cause bloat. Kephart (5), surveying the occurrence of bloat on sweet clover over a wide area, reached these conclusions:

1. Bloat is worse when the clover is succulent.
2. Bloat occurs most readily when the animal is hungry.
3. Bloat occurs when water or minerals or both are lacking or low.
4. Bloating is an individual matter, possibly because some animals are more greedy than others.

Our results do not support this theory of excessive gas formation: the amounts of gas formed on alfalfa hay and grain exceeded those formed on green alfalfa in a highly succulent stage, generally believed to be most conducive to bloat. In fact, bloat actually occurred during one test period on green alfalfa, though the amount of gas formed, as determined by actual test after this period of bloat, was less than during several other trials on hay alone or on hay and grain. We have shown, furthermore, that amounts of gas far exceeding those formed under any conditions studied may be introduced without serious effects. We conclude, therefore, that bloat is not caused merely by an excessive gas formation. The amount of food consumed and consequently the amount of gas formed is no doubt a contributing but not the main factor in producing bloat.

Toxic-Gas Theory.—We have no data to support or disprove Dougherty's theory that a toxic gas is responsible for death in bloated animals. The evidence on the amount of carbon monoxide formed in the rumen of animals on different rations (2, 8) does not strongly support this view. Dougherty (2), however, has conclusively proved that when carbon monoxide is pumped into the rumen, the gas diffuses into the blood, producing a condition somewhat similar to bloat. His theory really relates to the cause of death following bloat rather than to the cause of bloat.

Interference with Belching.—In our opinion, bloat is caused not by excessive gas formation but by interference with belching. If, for example, animals are pastured on beet tops, the lodging of a piece of beet in the esophagus results in rapid bloating if it is not removed. Surely this is merely the prevention of the escape of gas through the esophagus. Bell and Britton (1), furthermore, state that if lambs on legume pasture turn on their backs and are unable to rise, bloating occurs rapidly. Under these conditions, apparently, belching is prevented by submergence of the cardiac orifice. Conceivably, bloat on green alfalfa or grain alone may be explained by the fact that the rumen contents, being more liquid, cannot be packed away in the posterior rumen; the cardiac orifice becomes submerged, and belching is prevented.

In our opinion bloat most frequently results from absence of the stimuli necessary to initiate belching. As Schalk and Amadon (11) have shown, regurgitation is a reflex act depending upon the constant scratching of the walls of the rumen by roughage; they induced regurgitation artificially by rubbing a wisp of hay, introduced through a rumen fistula, over the inner walls of the rumen. In our opinion, the belching mechanism is controlled in a somewhat similar manner. As we have previously pointed out, belching occurs at the height of ruminal contraction and is correlated with the peak of ruminal pressure. Yet increased pressure in itself does not open the cardiac orifice, for when gas was artificially introduced, the pressure frequently rose much higher than in any normal animal, and yet gas escaped only during ruminal contraction. The invariable occurrence of bloat in ruminants after death also emphasizes that the release of gas from the rumen depends upon a functional reflex mechanism. The cardiac orifice is no doubt opened for gas to escape by a reflex mechanism. A relatively rapid change of pressure, such as occurs during ruminal contraction, is probably important; but in our opinion this stimulus must be augmented by the scratching of the rumen walls with roughage. There is evidence to support this belief: bloat occurs most readily under two conditions—the feeding of grain alone or the feeding of succulent legumes. In both instances the amount of prickly fiber present is at a minimum. Fibrous roughage is effective because prickly. Thus bloat seldom occurs on rations of hay and grain. As Mead and Goss (7) have shown, nonirritating fiber such as finely ground paper pulp added to a grain ration did not prevent frequent bloating. According to many field reports, if alfalfa hay is deprived of its prickly nature by fine grinding, bloat frequently occurs.

Evidently if the reflex mechanism to induce belching is faulty, the amount of trouble expected from bloat will depend to a marked degree upon the amount of gas produced, which in turn will vary with the

amount of feed consumed. If, on the other hand, the mechanism to induce belching is normal, then, as we have shown, the cow can belch not only the maximum amount of gas formed under natural conditions, but even greater amounts.

One may ask why bloat does not occur so frequently on the grasses as on the legumes. To this question, we must confess, we do not have a satisfactory answer. A tentative reply, until experimental work is done to clarify the point, is that grasses are perhaps ingested more slowly than legumes because of the nature of growth. Or lush-growing grasses may be more stemmy than legumes. Very occasionally bloat does occur on rank, succulent grasses such as barley.

To explain the chronic bloater by this belching-interference theory of bloat, we may assume that individuals differ in nervous irritability and that the chronic bloater has a high threshold of irritability. Even coarse roughage in the rumen may be insufficient, in such cases, to stimulate belching.

PREVENTIVE MEASURES AGAINST BLOAT

According to our theory, bloat results from a dietary lack of sufficient fiber of proper type to initiate belching. We suggest, accordingly, that enough roughage of a coarse, stemmy nature be included in the diet to overcome this deficiency or to prevent excess eating of succulent foods lacking in fiber. The result may be accomplished by several means, but in certain instances all the suggestions are impractical.

If animals are being fattened on legume pasture and grain, then chopped (but not finely ground) hay may be mixed with the grain. Some lamb feeders are now following this practice.

For both lamb and cattle feeding, it may prove desirable to mix grasses with legumes for pasture. According to Bell and Britton (1), "bloat was not a problem in pastures covered with more than 50 per cent of grasses."

Another desirable practice is to feed cattle, particularly lactating dairy cows, palatable hay before turning them into legume pasture. This practice has been carried on successfully with the milking dairy herd of the University Farm at Davis. One must remember that animals on excellent legume pasture may refuse hay unless it is of good quality. Because, furthermore, cattle consume hay rather slowly, they should have access to it for several hours daily. Lactating cows, which have a stronger appetite than nonlactating cows, will require special precautions. Rapidly growing animals, too, will be more greedy than mature nonlactating animals.

In years when luxuriant growth of forage occurs, there is trouble with bloat on the range, particularly when legumes constitute a major part of

the forage plants. We do not have a satisfactory solution for this problem of bloat on the range.

None of our advice on the prevention of bloat is original; one finds a host of suggestions in the literature. The difficulty has been in determining which of these to follow. We believe that sound experimental evidence underlies our suggestions.

SUMMARY AND CONCLUSIONS

Pressures within the rumen of a cow were studied by means of a specially devised plug for a ruminal fistula. Belching occurs when the pressure is raised in the rumen by means of an active contraction of the ruminal musculature. Increased pressure, in itself, does not force gas from the rumen through the esophagus, as is illustrated by the artificial introduction of gas into the rumen. The amount of ruminal gas formed, both in a cow with a ruminal fistula and in a normal cow, was determined on rations of alfalfa hay alone, on green alfalfa alone, and on hay and grain. The amount of gas formed is more closely correlated with the time after eating than with the nature of the ration and is directly related to the amount of feed eaten. The composition of rumen gas was the same irrespective of the type of feeds used in these experiments.

The theory is proposed that the expulsion of gas from the rumen by belching is a reflex mechanism dependent upon an adequate amount of fibrous material of a prickly nature. Succulent legumes and concentrates contain a minimum of fiber and are therefore particularly conducive to bloat. Preventive measures consist in the introduction of sufficient fiber in the ration to initiate belching.

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